

ROANELLA, A NEW ?BILLINGSSELLOID BRACHIOPOD
FROM THE LATE CAMBRIAN DOLODROOK LIMESTONES,
EAST-CENTRAL VICTORIA

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The new brachiopod genus *Roanella* is described from a large collection of silicified shells collected from Upper Cambrian (Idamean) limestones in the vicinity of Roan Horse Gully in the Dolodrook River watershed. The taxon is very similar to *Billingsella*, but is distinguished from it by the presence of a deltidium (rather than a pseudodeltidium) and absence of dental plates. The presence of a deltidium in *Roanella* is unique for the Billingselloidea. The restricted facies distribution, high density clustering, limited lateral and stratigraphic extent and high disarticulation index indicate *R. platystrophioides* was an opportunistic species that inhabited a high energy, shallow marine environment.

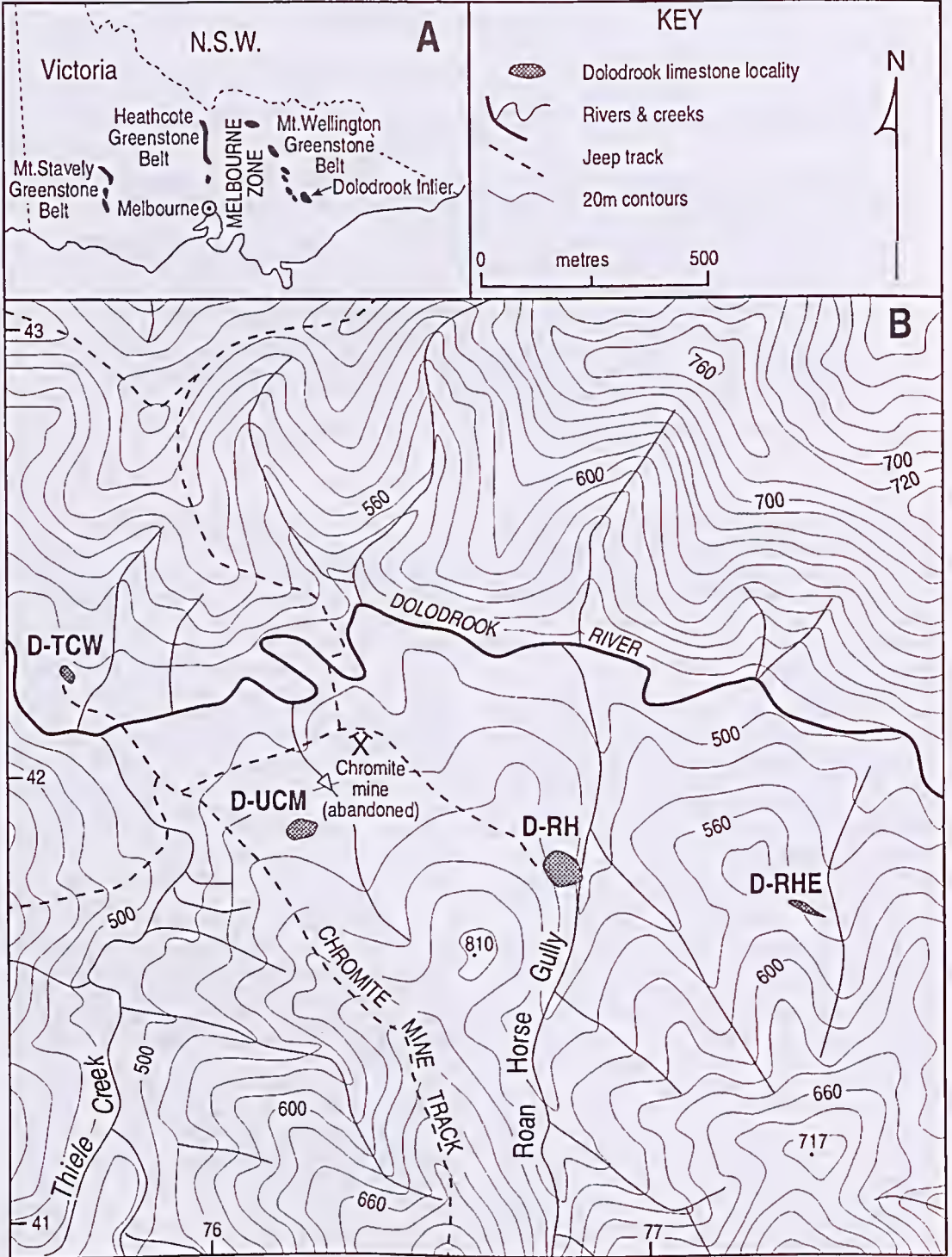
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CAMBRIAN fossiliferous localities in Victoria are almost exclusively restricted to small fault-bounded units, often with limited exposure, associated with the Heathcote and Mt Wellington greenstone belts, defining the western and eastern margins respectively of the Melbourne Zone (Crawford & Keays 1978; Crawford 1988) in the southwestern Laehlan Fold Belt (Glen 1992: fig. 2). The earliest descriptions of Cambrian fossils from Victoria focussed on the faunas of the *Dinesus* and *Amphoton* beds in the 150 m thick Knowsley East Formation in the Heathcote Greenstone Belt. These produced trilobites (Etheridge 1896; Gregory 1903; Chapman 1917; Öpik 1949), brachiopods and bivalves (Chapman 1904, 1917), and a relatively diverse dendroid graptolite assemblage (Chapman & Thomas 1936). Limestone bodies, some perhaps fault-bounded, of Middle-Late Cambrian age in the Dolodrook River Inlier of the Mt Wellington Greenstone Belt contain a diverse shelly fauna including trilobites (Harris & Thomas 1954; Thomas & Singleton 1956), lingulate brachiopods (Engelbretsen, in prep.), calciate brachiopods, molluscs, crinoids and algae (partly described by Chapman 1907, 1911). These faunas are either in need of revision or have not been formally described. As an initial step in this direction, the articulate brachiopod *Roanella platystrophioides* (Chapman) is redescribed, based on a large collection of silicified shells from three localities in the vicinity of Roan Horse Gully, a tributary of the Dolodrook River (Fig. 1).

PREVIOUS INVESTIGATIONS

Initial investigations into the geology and physiography of the Dolodrook River–Mt Wellington–Maeallister River area were undertaken by R. A. F. Murray (1879) and A. W. Howitt (1891), but it was E. O. Thiele (later Teale) who, during a series of reconnaissance excursions to the region (Thiele 1905–1908), first called attention to the Dolodrook limestones (Thiele 1907: 26) initially mapping them as Silurian units resting on top of, and surrounded by, Ordovician graptolite shales. The Silurian age was supported at the time by Chapman's (1907) identification of *Platystrophia bifurcata* (= *Roanella platystrophioides* herein). Teale (1920) later provided a comprehensive synthesis of the stratigraphy, geology and palaeontology of the region, revising much of his earlier work. The discovery of early Palaeozoic trilobites in four of nine limestone occurrences in the Dolodrook River watershed (Thiele 1908; Teale 1920; Chapman 1911), led Thiele to assume a broad Cambrian age for all the limestone occurrences in that area.

Teale (1920) recognised three groups of rocks in his pre-Ordovician (or Heathcotean) Series: pre-Upper Cambrian Serpentine, overlain unconformably by the Upper Cambrian trilobite (or Dolodrook) limestones, and bedded ash and tuffs, his Garvey Gully series, which he considered to be interbedded with the limestones (Teale 1920: 78).



Harris & Thomas (1954: 36) revised some of Teale's (1920) conclusions, indicating that the serpentine was probably 'not an older series but an essential part of the Cambrian sequence'. Apart from recovering Middle Ordovician graptolites from near the mouth of Roan Horse Gully and adding substantially to knowledge of graptolites in the area, Harris & Thomas (1954) also provided a list of trilobites identified by O. P. Singleton from the limestones at Roan Horse Gully and a locality on the Dolodrook River upstream from Black Soil Gully (see also Thomas & Singleton 1956). Little subsequent work has been undertaken in the region, apart from an unpublished honours thesis (Duddy 1974), though reference has been made to the area in broad regional syntheses (eg. VandenBerg 1988; Crawford 1988).

GEOLOGICAL SETTING

The geology of the Dolodrook Inlier, presented in meticulous detail by Teale (1920) has been modified in relatively minor ways by Harris & Thomas (1954), Duddy (1974) and Crawford & Keays (1978). It is part of the Mt Wellington Greenstone Belt (Fig. 1A), and outcrops as a broad, NW-SE striking, antilinerial structure with a core of serpentinised cumulate ultramafic rocks, including harzburgites and dunites (Crawford et al. 1984; Nelson et al. 1984; Crawford 1988); partially serpentinised conglomerates are also known (Crawford 1988). Cas (1983) argued that the Victorian greenstone belts were produced in intra-eratonie rift zones, but Crawford et al. (1984), Crawford & Keays (1987) and Crawford & Berry (1992: 38) have argued, based on comparison with modern western Pacific analogues, that the greenstones formed in an intra-oceanic arc and back-arc setting, and were subsequently thrust eraton-wards at some time prior to the Middle Devonian. Collins & Vernon (1994: 260, fig. 3a, b) have recently provided two models to explain development of the southern Lachlan Fold Belt: a sequential back-arc formation model, and a back-arc duplicate model involving strike-slip faulting.

The ultramafics are unconformably overlain by

the Garvey Gully Formation, an approximately 200 m thick unit of fine to medium-grained, poorly sorted green to grey volcanolithic sandstones, minor conglomerates and shales. Rounded monomineralic and polymineralic clasts are relatively common towards the base of the unit and are assumed to have been derived, in the main, from the underlying greenstone terrane (Duddy 1974; Crawford 1988: 54). The sandstones produce rare fragmentary echinoderm plates and crinoid ossicles and display various soft sediment structures including small scale crossbedding, scour surfaces, slumps, flame structures and channels (Duddy 1974) indicating deposition in a 'high energy', shallow marine setting.

The Dolodrook River limestones have been regarded as a thin, autochthonous unit interbedded within the upper part of the Garvey Gully Formation (Teale 1920; Duddy 1974; VandenBerg 1988; Crawford 1988). No type section appears to have been nominated. Lithological boundaries between the limestone outcrops and the Garvey Gully Formation are almost always obscured by soil cover or by localised faulting, but Duddy (1974) has reported the presence of a disconformable contact between the Garvey Gully Formation and overlying Dolodrook River limestone at his locality 109, in Black Soil Gully West. He (Duddy 1974) and subsequent authors, assumed no major stratigraphic break between the units. In accord with this view, VandenBerg (1988: 17, table 3-1) indicated the Dolodrook River limestone as a lithostratigraphic member of the Garvey Gully Formation, except that the latter is inferred by us (see below) to be mid-Ordovician rather than Cambrian in age. Recent discoveries of *Diplograptus* and *Didymograptus* from a locality in the Garvey Gully Formation arenites within metres, and along strike, from the Dolodrook River limestone (D-TCW) at Thiele's Creek (Fig. 1B), indicate a mid-Ordovician (Darriwilian) age for the formation. This previously unrecorded age discrepancy between the Cambrian limestones and the Ordovician Garvey Gully Formation can be adequately accounted for if the limestones are viewed as submarine carbonate channel deposits and/or debris flows and isolated olistoliths derived from cannibalisation of a shallow water carbonate

Fig. 1. A, Position of the Dolodrook Inlier in the Mt Wellington Greenstone Belt on the eastern margin of the Melbourne Zone. B, Location of relevant limestone bodies in the Dolodrook River area. Base map: 1:25 000 topographic map Tali Karg, 1st edn, 1990 (Vicmap). Universal 1000 m grid reference arc shown.

platform, deposited in a turbiditic environment, the Garvey Gully Formation. That trilobite faunas derived from the Dolodrook River limestones represent at least three distinct ages (see below) accords with a history of platform collapse, possibly episodic and triggered by tectonic events. It could also reflect the history of incision into deeper and older horizons on a now 'lost' carbonate platform. Because the limestone bodies of the Dolodrook River are an integral part of the Garvey Gully Formation and do not constitute a coherent stratigraphic unit within it, they are not accorded formal member status.

Of the eleven limestone outcrops sampled in the Dolodrook River area, only three seemingly fault-bounded lenses produced *Roanella platystrophioides* (Fig. 1B). The materials came from a sampled stratigraphic section on each body: D-RH, a 42.4 m section on the western flank of Roan Horse Gully commencing at 766₆417₅ on 1:25 000 topographic sheet Tali Karng; D-RHE, a 15 m section east of D-RH commencing at 770₂416₄; and, D-UCM, a 29.7 m section uphill southwards from the abandoned chromite mine commencing at 764₆413₉ (Fig. 1B).

The limestone on the western flank of Roan Horse Gully (D-RH; Fig 1B) is apparently fault-bounded on all sides; according to Duddy (1974) it has been thrust over Upper Ordovician slates. There is some uncertainty regarding facing of the limestone, but it is assumed to dip at 80°+ to the south, the presence of ultrabasics beneath the limestone according with younging to the south. There is apparently no development of the Garvey Gully Formation in this area; Duddy (1974) inferred that it had thinned or been faulted out.

Carbonate clasts up to 0.5 m across occur in a relatively coarse conglomeratic matrix about 200 m downstream along Roan Horse Gully from the presumed base of the limestone. The sequence appears to be part of the Mt Wellington Greenstone sequence but could be interpreted as anomalous Garvey Gully Formation represented by cannibalised ultramafics.

The petrology of the limestone in Roan Horse Gully has been commented upon briefly by Ebsworth (in Duddy 1974). The lower half of the limestone is dominated by algal pellets, with minor allochems consisting of trilobite debris, brachiopod shells and echinoderm ossicles. The original nature of the matrix is obscure, but now consists of recrystallised and/or dolomitised sparry calcite. The shells of *Roanella platystrophioides* are silicified in the lower half of the limestone. The upper half of the limestone tends to be massive, and contains few obvious bioclasts.

AGE OF THE DOLODROOK LIMESTONES

The trilobite faunas from the Dolodrook River limestones have never been formally described, though a species list was provided by Thomas & Singleton (1956); the whereabouts of the collections is presently unknown, presumed lost (D. J. Holloway, pers. comm.).

Dr Allison R. Palmer has provided one of us (GAB) with unpublished notes made during a re-evaluation of the Dolodrook trilobites on 13–14 April 1961, where the taxa listed by Thomas & Singleton (1956) were recognised by Palmer as a composite of at least 3 faunas. The oldest fauna, from limestone outcrops in Garvey Gully, is Middle Cambrian in age and represented by *Hypagnostus* (possibly 2 species), *Ptychagnostus australiensis* (Chapman), *Thielaspis thieli* (Chapman) (= *Mapania*?), a smooth agnostid and an indeterminate ptychopariid. This is followed by an upper Mindyallan (*Crepicephalus* Zone equivalent) fauna consisting of *Crepicephalus etheridgei* (Chapman), *Bynumia*, *Cedaria* cf. *gaspensis*?, a new elanoaspid genus and species, *Aspidagnostus*?, an indeterminate corynexochid, and a solenopleurid with a *Bonnia*-like tail. The youngest fauna, which includes material from Roan Horse Gully exposures, is basal Idamean (*Aphelaspis* Zone equivalent) and includes *Agnostus inexpectans*, *Pseudagnostus* sp., *Olenaspella separata*, *Pseudagnostina*?, *Aspidagnostus laevis*?, *Corynexochus* cf. *plunula*, *Aphelaspis*?, *Proceratopyge*? and a smooth agnostid.

FAUNAL COMPOSITION AND DEPOSITIONAL ENVIRONMENT

The fauna in the lower half of the Roan Horse Gully Section D-RH is dominated almost entirely by *R. platystrophioides*. Using the seven criteria outlined by Levinton (1970: 77), and elaborated by Alexander (1977), *R. platystrophioides* could be considered an opportunistic species based on its restricted facies distribution, overwhelming faunal dominance, high density clustering, limited lateral distribution, and restricted stratigraphic occurrence. Alexander (1977) noted that the majority of opportunistic species are characterised by comparatively small biovolume, conservative deposition of calcium carbonate (leading to small size and shell thicknesses of less than 1.0 mm), and initially rapid growth rates leading to early sexual maturity—the last inferred from the distance between successive concentric growth lines. Though

R. platystrophioides has a comparable biovolume to the opportunistic species *Billingsella perfecta* from the Late Cambrian St Charles Formation of Utah and Idaho (Alexander 1977), and falls within the size range of a typical opportunist (mean maximum length 8–17 mm), it tends to have a thicker pedicle valve (up to 2 mm thick), and a greater degree of radial costellation than taxa identified by Alexander (1977) as opportunists. In addition, concentric growth lines tend to be lacking in *R. platystrophioides*, making it impossible to determine the growth rate of this species.

It is clear that, like *B. perfecta*, *R. platystrophioides* was attached to the substrate by a few pedicle threads as a juvenile (or subadult), but during subsequent growth the foramen was gradually closed (by deltidial plates in the case of *R. platystrophioides*); the shell is therefore inferred to have been free-lying at maturity. Given the extra weight and size of the pedicle valve it would seem reasonable to suggest that it must have been in contact with (or partially buried in) the substrate during life. Because of the high level of shell disarticulation (97%), abrasion and breakage, combined with the presence of oncolites, numerous algal pellets, and rare rounded lithic clasts we infer that *R. platystrophioides* inhabited a high energy, periodically storm influenced, near shore environment, presumably algal-bound tidal flats. The thick shell would have provided protection in such a hostile environment.

Other fossils recovered from D-RH include isolated pelmatozoan columnals, spongiomorph spicules, aphelaspid trilobites (Laurie, in prep.), a few unidentifiable lingulate brachiopod fragments, and a small, solitary, cup-shaped, coral-like organism of uncertain affinity. The D-UCM section produced fewer *R. platystrophioides* specimens than D-RH, but also produced pelmatozoan columnals and fragments of an indeterminate high spired gastropod. Only a few silicified *R. platystrophioides* were obtained from the relatively small D-RHE section. Algal pellets are common in the lower half of all three limestone tracts.

SYSTEMATIC PALAEOONTOLOGY

All figured specimens are in the Museum of Victoria; catalogue numbers are indicated in the figure captions.

Phylum BRACHIOPODA Dumeril 1806

Subphylum RHYNCHONELLIFORMEA
Williams et al. 1996

Class STROPHOMENATA Williams et al. 1996

Order STROPHOMENIDA Öpik 1934

Superfamily ?BILLINGSSELLOIDEA
Schuchert 1893

Family UNCERTAIN

Discussion. Despite being typically 'billingselloid' in overall appearance, the delthyrial cover in *Roanella* is a deltidium (or symphytium in mature specimens) formed by conjunct deltidial plates (Figs 2F, L, R; 3B, H). All known species of *Billingsella* are described as having a pseudodeltidium; Walcott (1912: 305) stated emphatically that 'no deltidial plates are known in the Billingsellidac'. The ontogenetic development of the delthyrial cover in *Roanella* begins with discrete deltidial plates (Fig. 2F, L), followed by gradual growth of a well developed deltidium with a median line of suture in subadult specimens (Fig. 3B, H), to development of a deltidium that has lost the median line of suture, forming a symphytium in mature specimens (Fig. 2R; Williams & Rowell 1965: H86). The symphytium strongly resembles a pseudodeltidium, but the presence of deltidial plates in a large number of specimens of *Roanella* cannot be confused with the ventrally restricted, convex pseudodeltidium, typically formed as a single plate during early embryonic growth in strophomenidine brachiopods (Arber 1942; Williams & Hewitt 1977).

Because the Class Strophomenata, as presently defined (Williams et al. 1996), includes only taxa with a pseudodeltidium (see also Brunton & Cocks 1996), the presence of a deltidium, could be taken as evidence for excluding *Roanella* from the Strophomenata. The presence of a deltidium in *Roanella* may be interpreted in two ways: either *Roanella* is an aberrant billingselloid taxon that for some reason, in geographic isolation, developed a deltidium instead of a pseudodeltidium, or *Roanella* represents a stock that displays remarkable convergence with billingselloid morphology. In support of the first view is the observation that, apart from the presence of a deltidium, *Roanella* is almost indistinguishable from taxa currently assigned to *Billingsella*. Wright (1996), among others, has noted that morphological characters may be fluid in 'the early phases of evolution of a group'; the presence of a deltidium in *Roanella* may thus represent a significant but not order-level divergence from the rest of the billingselloid clade. The presence of laminar secondary shell in *Roanella* would provide further evidence in support of billingselloid affinity (Williams 1970), but this

cannot be ascertained because silicification has obliterated the original secondary shell structure in all available material.

On the other hand, the presence of a deltidium in *Roanella* may be taxonomically significant at a high level, possibly reflecting a heritage far removed from the billingselloid clade. Given the widespread occurrence of convergence among invertebrate groups (Moore & Wilmer 1997) the close phenotypic similarity between *Roanella* and *Billingsella* may simply reflect adaptation to a similar suite of environmental parameters (especially relevant given that both taxa display numerous adaptations that allow them to survive in high energy, shallow water environments). Cladistic methodology tends to disguise possible examples of convergence (see detailed discussion in Moore & Wilmer 1997)—a point that should be kept in mind given that all recent supraordinal classifications of the Brachiopoda are based on cladistic analysis. Thus, identification of possible instances of convergence at the level of genus and species is notoriously difficult and is entirely dependent on accurate identification of phylogeny.

Wright & Rubel (1996) have noted the presence of a deltidium in the clitaubonitidine brachiopods; it is thus possible that *Roanella* may be an early member of this lineage. However, the clitaubonitidines are characterised by the presence of a spondylium (assumed to be formed by the fusion of dental plates), and Wright (1996: A63) has indicated that 'the clitaubonitidines must have arisen from an as yet unidentified late Cambrian orthacean stock with dental plates'. It should also be noted, nevertheless, that there is uncertainty regarding the origin of the spondylium in clitaubonitidines; Wright (1996: A63) has conceded that this structure may have evolved from a 'pseudospondylium formed from the thickening on the valve floor between the dental plates'. Despite the absence of dental plates in *Roanella*, there is consistent and prominent shell thickening in the umbonal region (often forming a prominent anterior boss; Fig. 3B, C, H, I), that may have been the precursor to an early spondylial structure.

What then can we conclude about the affinities of *Roanella*? If a billingselloid affinity is advocated, and the provisional placement of the Billingselloidea with the orthotetidine strophomenids by Williams et al. (1996) is accepted, then *Roanella* may be regarded as an aberrant strophomenoid with a deltidium. Williams et al. (1996: 1183) also placed the clitaubonitidines as a suborder in the Order Strophomenida and suggested that the deltidium in these brachiopods does not preclude assignment to the Class Strophomenata. *Roanella* can therefore also be viewed as a strophomenate brachiopod with a close affinity to the billingselloids. A deltidium has been reported previously in only a few early Palaeozoic orthoids, for example *Barbarorthis*, *Campylorthis* and *Tuvaella*, and though the possibility of convergence cannot be completely ruled out, the weight of morphological evidence indicates that *Roanella* is an unusual taxon exhibiting a combination of billingselloid and clitaubonitidine features. The presence of characters more typical of the billingselloid clade (such as the vascular system and brachial valve morphology) suggests *Roanella* should be assigned tentatively to the Billingselloidea, though the family-level assignment is left open.

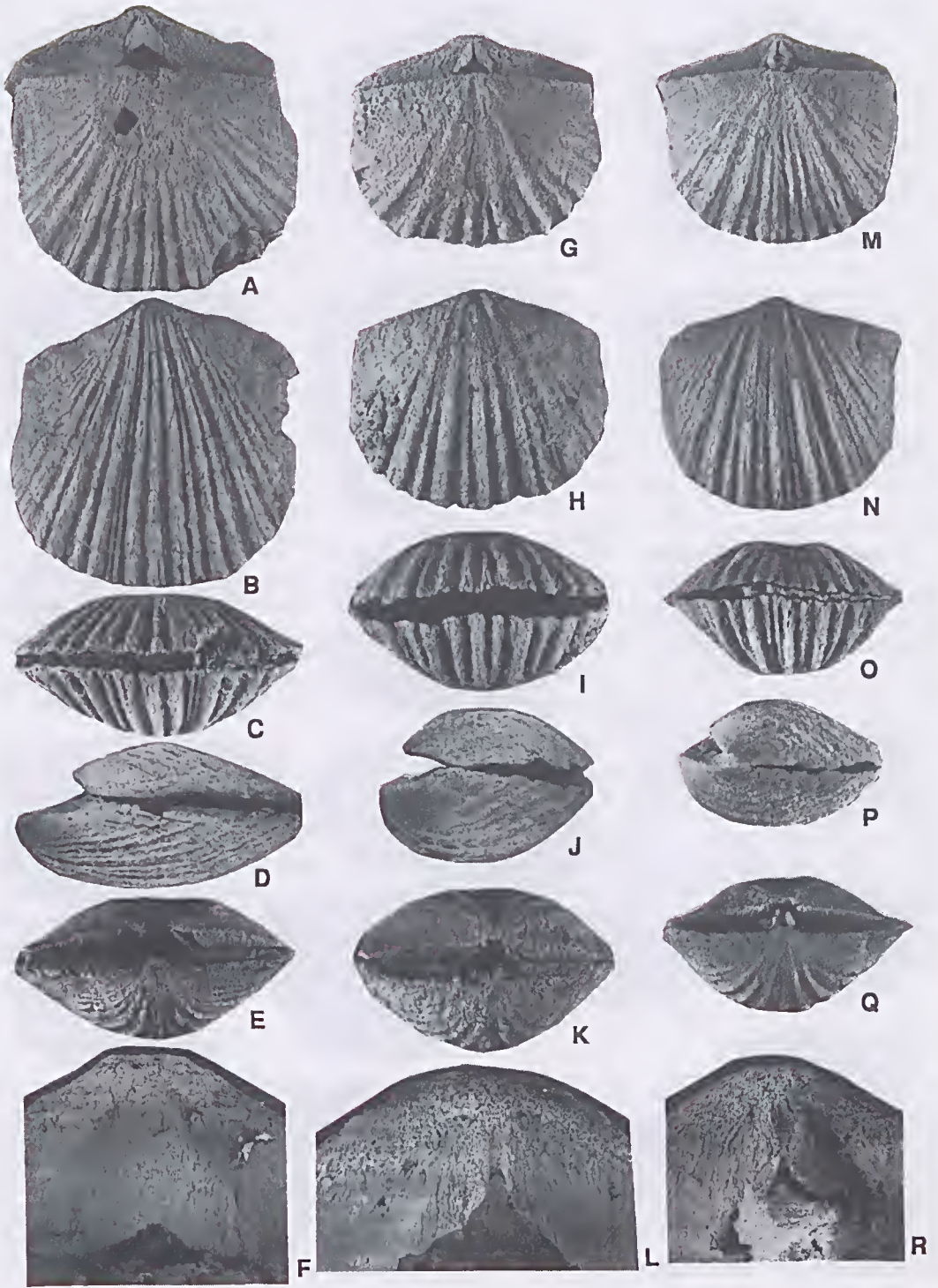
Roanella n. gen.

Type species. *Roanella platystrophioides* (Chapman 1911: 311, pl. 59, figs 14, 15; pl. 60, fig. 24).

Etymology. After Roan Horse Gully, the type locality.

Diagnosis. Small (maximum width 17 mm), ventri-biconvex, unequally costellate shell with semi-circular to subquadrate outline. Pedicle valve thick-shelled, mostly with sharply alate hingeline; delthyrial cover formed by coalescence of deltidial plates to form a deltidium or symphytium; teeth small, poorly defined, lacking dental plates; ventral muscle field deeply impressed with raised median boss defining anterior margin of field, mantle canal system saecate. Brachial valve lacking chilidium.

Fig. 2. Articulated specimens of *Roanella platystrophioides* (Chapman). All specimens from D-RH 21.7. A-E, Dorsal, ventral, anterior, lateral and posterior views of NMV P148697, $\times 3.5$. F, Enlargement of symphytium of NMV P148697, $\times 15$. G-K, Dorsal, ventral, anterior, lateral and posterior views of NMV P148698, $\times 6$. L, Enlargement showing disjunct deltidial plates of NMV P148698, $\times 16$. M-Q, Dorsal, ventral, anterior, lateral and posterior views of NMV P148699, $\times 6$. R, Enlargement showing disjunct deltidial plates of NMV P148699, $\times 22$.



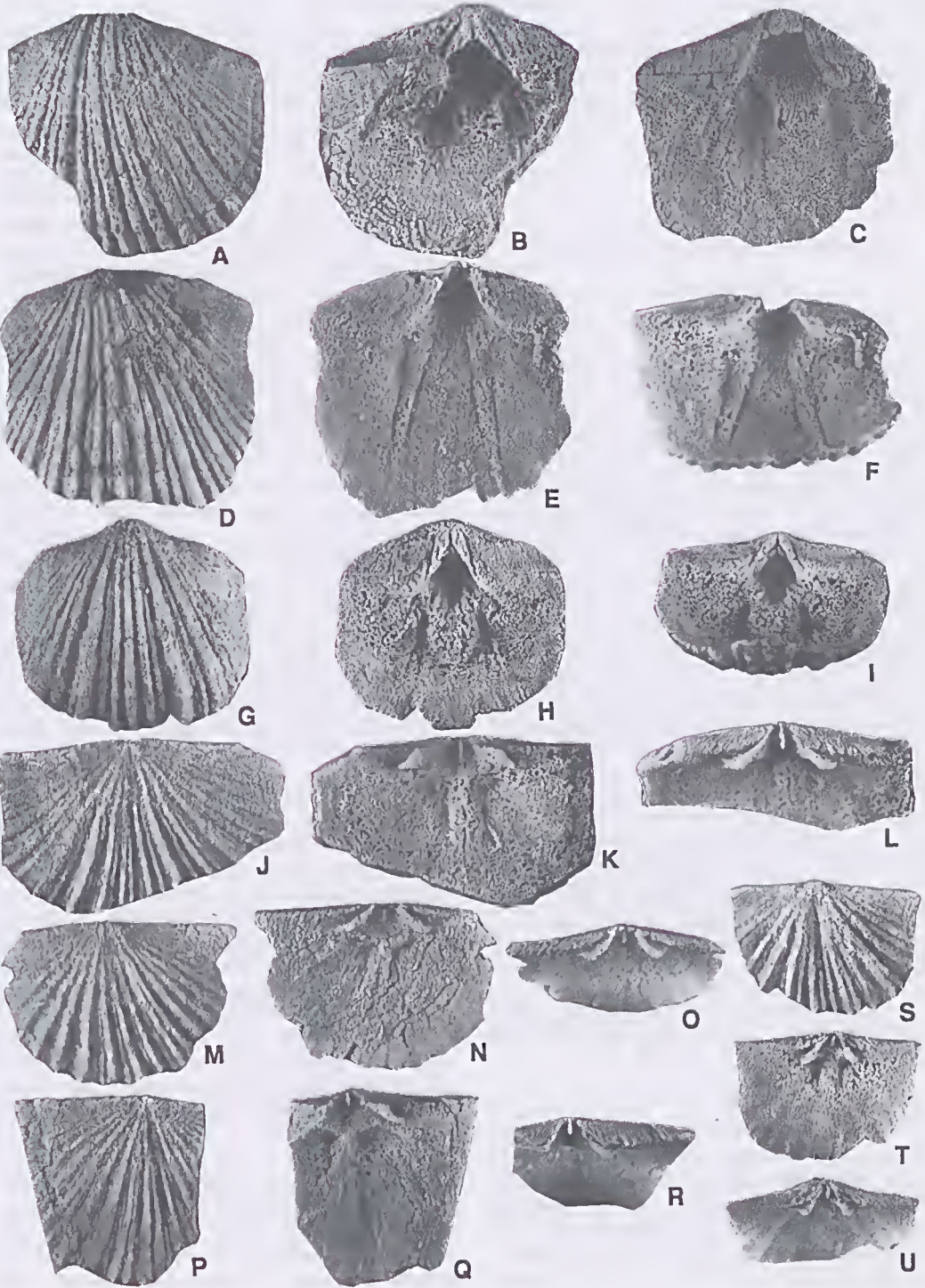
Discussion. The distinction between deltidial plates and lateral plates is not immediately apparent, though the latter term has rarely been used in descriptions by more recent workers. Schuchert & Cooper (1932: 22–23) reported the development of 'lateral plates' overlapping a 'stiffened' pseudo-deltidium in some orthoids (eg. *Hesperorthis*), and though the umbo of *Roanella* is filled with thickened deposits of secondary shell material (similar to *Billingsella*) under the deltidium, this should not be confused with a true pseudo-deltidium (see Arber 1942). Schuchert & Cooper (1932) stated that 'lateral plates' never join in the median plane and can thus be distinguished from deltidial plates, but the two are here regarded as essentially synonymous. The deltidium in *Roanella* is also comparable to the so-called notodeltidium in the Middle Devonian genus *Phragmophora* described and illustrated by Cooper (1955: 52, pl. 14A, figs 1–7). However, the notodeltidium completely fills the delthyrium in *Phragmophora* (Williams & Rowell 1965: H148) whereas in *Roanella* the deltidium occupies only the apical $\frac{1}{2}$ – $\frac{1}{3}$ of the delthyrium (Figs 2A, F, G, L, M, R; 3B, H), and eventually seals the foramen.

Roanella can be distinguished from *Billingsella* by the presence of a deltidium in the former; this feature alone is probably significant enough to warrant erection of a new billingselloid family based on *Roanella*, though brachial valves of the two genera are essentially indistinguishable (see Fig. 3J–U). It should be noted that evidence is mounting to suggest that *Billingsella* is probably an amalgam of at least two (possibly more) genera. The concept of the genus *Billingsella* has been detailed by various authors (Walcott 1905: 227, 1912: 749; Schuchert & Cooper 1932: 48–49; Ulrich & Cooper 1938: 72; Bell 1941: 245; Nikitin 1956: 24; Williams & Wright 1965: H305; Freeman & Stitt 1996: 359). Many workers have documented the substantial morphological plasticity of *Billingsella* (eg. Schuchert & Cooper 1932; Bell 1941; Bell & Ellinwood 1962; Mackinnon, in

Shergold et al. 1976; Freeman & Stitt 1996) noting the variable development of radial ornament, dental plates, cardinal process, chilidium, vascular markings and apical foramen. Laurie (1997), for example, has noted the fundamental difference between the mantle canal patterns exhibited by *B. plicatella* Walcott which has a digitate mantle canal system in the brachial valve and a saccate mantle canal system in the pedicle valve (see Bell 1941: pl. 34, figs 4–12; Williams & Wright 1965: fig. 135g), and *B. perfecta* which is characterised by a digitate mantle canal system in the pedicle valve. Such differences in vascular markings have recently been used to discriminate new genera of closely related orthoids (Jaanusson & Bassett 1993) and elitambonitidines (Wright & Rubel 1996). In addition, the lack of dental plates in all published species assigned to *Billingsella* from the Southern Hemisphere contrasts significantly with the development of prominent dental plates in most North American species, including the type species (see Schuchert & Cooper 1932: 28). The occasional description of a symphytium in *Billingsella* (eg. Cowen 1969) also raises the possibility that some specimens may, in fact, be related to *Roanella*. Though it is clearly beyond the scope of the present paper to review all taxa currently assigned to *Billingsella*, such a revision could potentially distinguish new taxa and help clarify early evolutionary trends within the Billingselloidea, a clade which is currently thought to be the stem group of the Class Strophomenata (Williams et al. 1996: fig. 6).

Roanella, in common with the billingselloid genera *Cymbithyris* Cooper 1952 and *Xenorthis* Ulrich & Cooper 1938 lacks dental plates, but *Cymbithyris* has a concavo-convex shell (Cooper 1952: 5, pl. 1B, 16, 20), and *Xenorthis* has a distinctly uniplicate commissure. *Saccogonum* Havlicek 1971 has a finer, multicostellate ornament and shorter vascula media than *Roanella* (see Cornee et al. 1987: 521–522, pl. 1A–D). Mergl et al. (1998) also report the presence of a pseudo-

Fig. 3. Pedicle and brachial valves of *Roanella platystrophioides* (Chapman). All specimens from D-RH 21.7 with magnification $\times 3.5$. A–B, Exterior and interior of pedicle valve NMV P148700 (note presence of disjunct deltidial plates and billingselloid-like vascular markings). C, Interior of NMV P148701. D–F, Exterior, interior and oblique interior of NMV P148702 with strong vascula media (note deltidial plates broken away in this specimen). G–I, Exterior, interior and oblique interior of NMV P148703 with more rounded outline and deep umbonal cavity bordered anteriorly by well developed median boss. J–L, Exterior, interior and posterior of NMV P148704 (note blade-like cardinal process and short median ridge). M–O, Exterior, interior and posterior of NMV P148705. P–R, Exterior, interior and posterior of NMV P148706. S–U, Exterior, interior and posterior of juvenile specimen, NMV P148707.



deltidium and short dental plates in species of *Saccogonum* from Morocco. The poorly known *Eosotrematorthis* Wang from the Arenig of northern China (Wang 1955) is apparently more strongly costellate than *Roanella* (see Williams & Wright 1965: H306). *Ocnerorthis* Bell 1941 is also similar to *Roanella*, especially in juvenile stages, but can be distinguished by its open delthyrium and elevated dorsal median ridge (Bell 1941: 252).

Roanella platystrophioides (Chapman)

Figs 2A–R; 3A–U

Platystrophia biforata (Schlotheim 1820); Chapman 1907: 34.

Orthis (*Plectorthis*) *platystrophioides* Chapman 1911: 311, pl. 59, figs 14, 15; pl. 60, fig. 24.

?*Eoorthis platystrophioides* Chapman 1917: 96.

Material. Chapman (1911) did not designate a holotype from his collections. His illustrated specimens (syntypes NVM P12312–P12315; Chapman 1911: pl. 59, figs 14–15; pl. 60, fig. 24) are poorly preserved and display only external morphology. Specimen NVM P12314 a ventral valve, illustrated by Chapman (1911: pl. 60, fig. 24—centre specimen on bottom row) is here designated as the lectotype. Specimens NVM P12312, NVM P12313 and NVM P12315 become paralectotypes. No information on internal morphology or the delthyrial cover can be ascertained from this type material making it impossible to adequately clarify taxonomic relationships. However, the material derived from the type locality in Roan Horse Gully by the authors is represented by abundant, well preserved silicified shells detailing internal and external morphology and ontogeny. Eleven specimens (NMV P148697–P148707) are illustrated herein. The collections also contain 371 brachial valves (NMV P148708), 1519 pedicle valves (NMV P148709) and 34 complete shells (NVM P148710) from the type locality, D-RH/21.7. In addition, 74 brachial valves (NVM P148711), 160 pedicle valves (NVM P148712), and 28 complete shells (NVM P148713) come from D-UCM/10 and 3 brachial valves (NVM P148714) and 44 pedicle valves (NVM P148715) from D-UCM/13.8.

Type locality. Limestone tract outcropping on the western flank of Roan Horse Gully at 766,417_s on the 1:25 000 topographic sheet Tali Karnig (see Fig. 1B).

Diagnosis. As for genus.

Description. Shell small (maximum width 17 mm), dominantly ventribiconvex, semicircular to subquadrate in outline; maximum shell width generally at hingeline in alate specimens, and at midlength in some non-alate specimens; anterior commissure rectimarginate to faintly sulcate; radial ornament unequally costellate, consisting of 7–12 rounded

primary costellae, with thinner, secondary costellae arising primarily by intercalation; growth lamellae not preserved.

Pedicle valve up to 2 mm thick. Interarea wide and long, flat or gently concave in profile, triangular and apsacline, cleft medianly by a wide, V-shaped delthyrium subtending an angle of 60–70°; deltidium or symphytium arched, covering apical $\frac{1}{3}$ – $\frac{1}{2}$ of delthyrium; foramen poorly declined, tiny or completely lacking (overgrown); teeth simple, small, blunt, lacking dental plates; ventral muscle field large, deeply impressed, occupying entire floor of umbonal chamber, extending up to 50% shell length, with anterior margin raised and thickened by secondary shell to form a pronounced rounded boss; Mantle canal system saccate, vaseula media strongly impressed, arcuate, originate either side of the boss at the anterior margin of the ventral muscle field, extending approximately 80% shell length, then (in one specimen) curving posterolaterally to become parallel with the valve margin.

Brachial valve with well defined, long, narrow, anacline interarea; notothyrium open; chlidium lacking. Notothyrial cavity with well developed, raised platform bisected medianly by simple, narrow, ridge-like cardinal process; sockets large, deep and cylindrical, excavated into posterior shell wall, but partly floored in some specimens by small 'fulcral' plates. Socket ridges short, massive, tusk-like; median ridge short, wide, low, occurring under, and anterior to the notothyrial platform, and merging imperceptibly with the shell floor; musculature and mantle canal system unknown.

Ontogeny. Large numbers of individuals from Roan Horse Gully show that smaller shells (<5 mm) tend to be weakly equibiconvex with a shallow, but distinct median sulcus on the brachial valve; the shell outline also tends to be more rounded and equidimensional. As the shell increases in size the outline tends to become more subquadrate and the shell more transverse. The pedicle valve becomes thicker and deeper, giving the shell a ventribiconvex lateral profile. The sulcus in the brachial valve gradually becomes weaker until it is almost imperceptible. At no stage during growth is a fold developed on the pedicle valve, though larger specimens sometimes develop a faintly sulcate commissure.

Discussion. Chapman (1907) originally misidentified this taxon as the species *Platystrophia biforata* (Schlotheim, 1820), based on comparison with shells also misidentified as *P. biforata* from the allochthonous Early Devonian limestones at Deep

Creek, east of Walhalla, Victoria. However, after the discovery of Upper Cambrian trilobites in limestones from the Dolodrook River, the taxon was redescribed by Chapman (1911) as *Orthis* (*Plectorthis*) *platystrophioides* n. sp. The limited number of specimens upon which Chapman (1911) based his description are in poor condition, consisting entirely of articulated specimens mechanically 'cracked out' of limestone. No description of the interior of this species was provided by Chapman (1911). Recovery of large numbers of well preserved silicified specimens from the Roan Horse Gully locality from which Chapman's material came has provided an opportunity for re-evaluation of the systematic position of this form.

Chapman's assignment of this form to *Orthis* (*Plectorthis*) was undoubtedly based on the biconvex, strongly costellate nature of the shells and the belief that it had a large open delthyrium (Chapman 1911: 311). He also noted the presence of an incurved beak and median fold on the pedicle valve. None of the 1733 silicified pedicle valves in the current collections display any evidence of a median fold or an incurved beak (see for example Fig. 2D, J, P). Chapman (1917) later transferred this species to *Eoorthis* based on specimens collected from the Knowsley East Formation at Heathcote, but did not illustrate the material or explain the reason for re-assignment to *Eoorthis*.

R. platystrophioides generally lacks a functional foramen; in this respect it is similar to many species of *Billingsella* (Freeman & Stitt 1996). In the few specimens with a foramen, it is so tiny that it is difficult to envisage it as a conduit for a functional pedicle. Ulrich & Cooper (1938: 72) commented upon the unusually small size of the foramen in *Billingsella* and hypothesised that the 'pedicle must have been a mere thread or perhaps a bundle of threads which serve to attach the animal to floating objects or possibly to the bottom'. That many species of *Billingsella* occur as monospecific populations, often associated with sedimentary structures indicative of shallow, turbulent environments (eg. oncolites) does not accord with a floating lifestyle. Ulrich & Cooper (1938: 72) noted that a similar sealing up of the foramen occurred in the elitambonitidine species *Estandia* and *Clitambouites*.

R. platystrophioides can be distinguished from the bulk of *Billingsella* species described from the Middle and Upper Cambrian of North America, such as *B. pepina* (Hall), *B. perfecta* Ulrich & Cooper, *B. coloradoensis* (Shumard), *B. rectangulata* Cooper and *B. corrugata* Ulrich &

Cooper by its coarser costellate ornament, lack of concentric growth lamellae and, more importantly, the presence of a deltidium and lack of dental plates (Fig. 3F, I). Dental plates are well developed in most North American *Billingsella* species, eg. *B. perfecta* (Ulrich & Cooper 1938: pl. 7, figs 11, 20–21; Bell 1941: pl. 35, figs 1, 4–5, 10–14), and *B. rectangulata* (Cooper 1952: pl. 1, figs 11, 13–15). Nikitin (1956) described several *Billingsella* species from the Cambrian of Kazakhstan, but most exhibit finer costellation than *R. platystrophioides*, or are significantly larger in size. *B. destombesi* from the Middle Cambrian of Morocco (Mergl 1983: 338, pl. 1, figs 13–16) is larger than *R. platystrophioides*, and can be distinguished by its strong, short, dental plates, finer radial costellae and longer median ridge in the brachial valve.

The few species of *Billingsella* previously described from the Southern Hemisphere are based on limited and/or poorly preserved material (often tectonised moulds in shales), making comparison with *Roanella* difficult. Percival (in Powell et al. 1982: 147–148, fig. 12, 1–5) described *Billingsella* sp. from the Upper Cambrian (Idamean) Cupala Creek Formation in western NSW and, despite the limited material and preservation as internal moulds, this species can be distinguished from *R. platystrophioides* on the basis of its dorsi-biconvex shell, finely multicostellate ornament and 'prominent widely-spaced concentric growth lamellae'. The *Billingsella* species from the Cupala Creek Formation is probably conspecific with *Billingsella* sp. indet. of Mackinnon (in Shergold et al. 1976: pl. 38, figs 11–19) from the Middle–Late Cambrian Mariner Formation, Northern Victoria Land, Antarctica (Percival, in Powell et al. 1982; Rowell, in Henderson et al. 1992). Mackinnon (in Shergold et al. 1976: pl. 38, figs 17–18) recovered a juvenile brachial valve of this species with a strongly developed median ridge extending to the anterior margin of the valve. A comparable ridge does not occur in brachial valves of *R. platystrophioides* of similar size.

Billingsella sp. 1 of Jago (1989: 40, pl. 2, figs A–J) from the early Late Cambrian (Idamean) Singing Creek Formation, Deniston Range, south-western Tasmania, can be distinguished only on external features, there being little information on interior structure. It has a subtrapeziform shell, fine parvicostellate radial ornament, and a pedicle valve with a low median fold and 'slightly concave posterolateral slopes' (Jago 1989: 40).

The taxon closest to *R. platystrophioides* is *B. cf. borukaevi* described by Rowell (in Henderson et al. 1992: 256, pl. 4, figs 1–5) from the early

Late Cambrian (Idamean) Minaret Formation, Ellsworth Mountains, West Antarctica. The shell dimensions, convexity, outline and radial ornament are indistinguishable from *R. platystrophioides*, even to the extent that Rowell (in Henderson 1992: 256) describes similar variation in the position of the maximum shell width, depending on the auriculate nature of the hingeline. Rowell (in Henderson et al. 1992) describes the presence of a pseudodeltidium in *B. cf. borukaevi* but, given the indifferent preservation and the limited material, it is possible that a symphytium rather than a pseudodeltidium is present. Unfortunately, the interior of the pedicle valve is not known in *B. cf. borukaevi* so no information is available on the dental plates nor the configuration of the muscle field and vascular system. However, *B. cf. borukaevi* can be distinguished from *R. platystrophioides* by the development of a 'broad conspicuous [median] ridge' extending 'to near the midlength of the valve' in the braehial valve of the former (Rowell, in Henderson et al. 1992: pl. 4, fig. 1). In contrast, the median ridge in the braehial valve of *R. platystrophioides* is merely a buttress under the notothyrial platform, and extends less than $\frac{1}{3}$ shell length (Fig. 3K, N, Q, T). *B. borukaevi*, originally described by Nikitin (1956: 30–31, pl. 2, figs 1–20), can be distinguished from *R. platystrophioides* by its dorsibiconvex profile and flatter pedicle valve.

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